Reviews

Conserving mobile species

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The distributions of many species are dynamic in space and time, and movements made by individuals range from regular and predictable migrations to erratic, resource-driven nomadism. Conserving such mobile species is challenging; the effectiveness of a conservation action taken at one site depends on the condition of other sites that may be geographically and politically distant (thousands of kilometers away or in another jurisdiction, for example). Recent work has shown that even simple and predictable linkages among sites caused by "to-and-fro" migration can make migratory species especially vulnerable to habitat loss, and substantially affect the results of conservation prioritizations. Species characterized by more erratic or nomadic movements are very difficult to protect through current conservation planning techniques, which typically view species distributions as static. However, collaborations between migration ecologists, conservation planners, and mathematical ecologists are paving the way for improvements in conservation planning for mobile species.

In a nutshell:

- Mobile species require new approaches in conservation planning
- Accounting for the dependencies among sites and populations is vital for successful conservation of mobile species
- Decision-theoretic approaches allow robust conservation decisions to be made, even in cases where migrations are poorly understood

Conservation planning has tended to assume that the targets of management, such as species or ecosystems, are static in space and time (Pressey *et al.* 2007). However, more than 12% of the world's vertebrates make long-distance movements, whether migratory or nomadic, and mobile species occur on every continent and in every ocean (Robinson *et al.* 2009). Theory for conserving mobile species is in its infancy, and there are only a few examples of conservation planning for migratory or nomadic species (Martin *et al.* 2007; Grantham *et al.* 2008; Klaassen *et al.* 2008; Sawyer *et al.* 2009; Sheehy *et al.* 2011; Singh and Milner-Gulland 2011; Iwamura *et al.* in press). Here, we address some of the issues specific to conservation planning for mobile species, review progress so far in solving those issues, and present an associated research agenda.

Movements by mobile species vary from regular "to-and-fro" migrations to less predictable, resource-driven nomadic wanderings. Some species exhibit irregular long-distance irruptions, driven by peaks or troughs in resource availability, while others perform

complex intergenerational relays (Table 1). Mobile species can perform important ecosystem functions (e.g. regulating prey abundance or delivering nutrient inputs) and conserving movement as a process may be just as important as conserving the species themselves (Shuter *et al.* 2011).

Accounting for dependencies among sites

The benefits of conservation actions for mobile species taken in one place (eg the designation of a protected area) depend on the magnitude of threats and the success of actions taken elsewhere, making it difficult to evaluate the conservation value of any particular location in isolation (Martin *et al.* 2007; Iwamura *et al.* 2013). In the extreme, if all individuals of a species regularly move between two areas, the area in more critical condition (ie characterized by a lower carrying capacity or where reductions in birth rate or survivorship are greater) will dictate the overall status of the species (Figure 1; see Sutherland 1996), and conservation measures taken in the less critical area could be redundant. Although possibly occupied only for a short period of time, stopover sites or drought refuges could also be crucial to a large proportion of the population; thus, a relatively small amount of habitat loss could, in theory, lead to rapid extinction (Figure 2; Weber *et al.* 1999). For example, the number of migratory shorebirds using the East Asian–Australasian Flyway (EAAF) has declined dramatically in the past few decades, and evidence implicates habitat loss at important stopover sites in the Yellow Sea (Murray *et al.* 2014). If this hypothesis is correct, then action to manage shorebird habitat elsewhere in the Flyway might fail to halt the decline of these birds without corresponding management at stopover sites in eastern Asia (Figure 3). Similarly, the migratory leatherback sea turtle (*Dermochelys coriacea*) is declining as a result of a combination of egg-poaching at its nesting sites and mortality from both inshore fisheries and pelagic long-line fishing. International restrictions on pelagic long-line fishing will not halt the decline of this species without corresponding effort at inshore locations and nesting sites (James *et al.* 2005).

Despite these dependencies among sites, mobile species may be able to avoid degraded sites as well as some of the impacts of habitat loss by virtue of their ability to travel long distances. Indeed, an assessment of species included on the International Union for Conservation of Nature (IUCN) Red List suggests that mobile species are not more likely to be classified as globally threatened and are not being added to the IUCN Red List at a faster rate than sedentary species (Kirby *et al.* 2008). However, this finding might simply be a function of the comparatively large geographic range size of migrants, and further theoretical and empirical investigation is required to understand whether mobile species are, as a general rule, more or less vulnerable to threats than their sedentary counterparts. Moreover, alterations already observed in migratory timing and routes in response to habitat loss and climate change underscore the urgent need for conservation practitioners to understand the extent to which mobile species can dynamically respond to these threats (Kirby *et al.* 2008; Cox 2010).

Choosing conservation areas for sedentary species commonly involves identifying the locations that collectively, and for least cost, contain the greatest number of species or largest amount of suitable habitat (Moilanen *et al.* 2009). Site selection for mobile species is necessarily more complex. First, calculating the spatial configuration of sites may involve not just one type of habitat or resource but several, all of which must yield suitable resources at the appropriate time and have the proper spatial configuration. For instance, many migratory ungulate populations have declined worldwide, even where species are well represented in protected areas (Craigie *et al.* 2010). Some protected areas have been shown to inadequately represent crucial resources, such as prerequisite conditions for breeding, or the full pathway of traditional migration routes required by the animals (Bolger *et al.* 2008). Second, priority

areas for mobile species may not be the breeding or non-breeding grounds but rather the migratory corridors, bottlenecks, or refugia – regions that are crucial to a large proportion of a population at some comparatively brief point in their life cycle (Buler and Moore 2011); for example, recent tracking studies have revealed that Mongolian saiga (*Saiga tatarica mongolica*) are funneled through narrow corridors during migration as a result of steep topography (Figure 4). Threats to these bottlenecks could cause major changes to metapopulation dynamics and survivorship for this critically endangered species. Similarly, human encroachment and changes in agricultural practices in southern Africa are restricting access to traditional migration routes, resulting in marked declines of ungulates and long-lasting impacts to ecosystems (eg changes in nutrient cycling and predation pressure; Fynn and Bonyongo 2011). Even relatively intact migratory routes face imminent disruption from continued, human-induced disturbances to land- and seascapes (Singh and Milner-Gulland 2011).

Large-scale conservation initiatives struggle to address migratory connectivity, despite considerable focus on the specific conservation needs of migrants in the literature. For instance, the US National Fish, Wildlife, and Plants Climate Adaptation Strategy (Small-Lorenz *et al.* 2013) does not address the needs of migratory species in climate-change vulnerability assessments; similarly, despite being responsible for managing a large number of charismatic migrants, the US National Park Service has yet to develop a comprehensive plan to deal with migratory species (Berger *et al.* 2014).

Conservation objectives for mobile species

Here we present an overview of the tools and approaches that may prove useful in conservation planning for migratory species. While there have been few working examples of spatial prioritization for conserving migratory species, the needs of migrants can, to a certain extent, be incorporated into existing frameworks,. The approach taken will depend on objectives influenced by both the ecology of the species of interest and factors such as project timeframe, budget, and expertise.

Objectives in conservation planning for mobile species must explicitly account for the movement of individuals. Current approaches for sedentary species tend to treat the distribution of each species as a single conservation feature (Rondinini *et al.* 2006; Moilanen *et al.* 2009). These approaches could be adapted to meet the needs of migrants simply by treating different parts of the movement cycle (eg breeding grounds, non-breeding grounds, and stopover sites or migration corridors) as separate conservation features. Information on the locations of sites and resources used by mobile species is often readily available, and where it is not, species distribution modeling or consultation with experts (ie expert elicitation; Martin *et al.* 2012a) can help generate predictions of distributions from available data. However, such approaches may fail to protect subpopulations where there is strong population segregation between sites, and may fail to allocate conservation actions to bottlenecks that support a disproportionately large part of the population at certain times.

Objectives that go one step farther – by considering the connectivity between different parts of the movement cycle – can help to avoid functionally important areas being omitted from conservation plans. Martin *et al.* (2007), for instance, used a decision theory approach to model a conservation strategy for the American redstart (*Setophaga ruticilla*), a bird that migrates between breeding grounds in North America and non-breeding grounds in Central America (Figure 5). Protected area placement was compared under two conservation objectives: maximizing the population size across the non-breeding distributions without consideration of the connectivity between the breeding and non-breeding sites, and maximizing the population size across the entire range by adding the constraint that maintained a minimum of 30% of a population in each of five breeding regions. The resulting

conservation strategies for each objective were highly divergent, with redstart populations in one of the five breeding regions very poorly protected when connectivity was ignored..

Information on migratory connectivity has been incorporated into conservation planning in both the marine (Moilanen *et al.* 2008; Linke *et al.* 2011) and terrestrial (Martin *et al.* 2007; Klaassen *et al.* 2008) realms, although effective working examples are rare. Existing prioritization approaches can be adapted where connectivity is both spatially continuous (Kool *et al.* 2013) and geographically discrete (Beger *et al.* 2010), as are the migrations of many bird species. Advances in tracking technologies, genetic approaches, and stable isotope analysis are proving to be useful tools for identifying connectivity among sites (Webster *et al.* 2002), and consultation with experts can fill in gaps where such information is not available. For example, the synthesis of expert opinions on the structure of EAAF migration routes for shorebirds enabled the identification of locations that supported cost-effective habitat management in the face of sea-level rise (Iwamura *et al.* in press).

Threats from global change – particularly climate change – can have complex and unforeseen impacts on population dynamics in migratory species, and conservation success may be dependent on understanding and managing the impacts of these threats on factors such as fecundity and survival (Cox 2010; Webster 2002). Innovations in demographic modeling (Frederiksen *et al.* 2014), mechanistic modeling of migration (Bauer and Klaassen 2013), and spatial population models (Naujokaitis-Lewis *et al.* 2013) have led to improvements in how to map movements of mobile species and their population dynamics across the full life cycle. Understanding the links between environmental factors and species demography allows us to distinguish often unanticipated threats and identify conservation actions with the greatest population impact. Such modeling is particularly important in networks with complex population flow dynamics and low mixing of subpopulations between sites, and in species for which habitat degradation is more of a threat than habitat loss. Because of their current reliance on specialized analysis and intensive collection of demographic data, such approaches will likely only ever be applied in single-species management of highly threatened species. However, advances in the statistical tools available for the interpretation of extensive datasets (such as those generated by citizen science eg eBird; http://ebird.org/) may broaden the applicability of these intensive approaches (Zipkin *et al.* 2014). Nonetheless, despite major advances in the ability to model species' responses to threats and environmental conditions, conservation ecologists are far from being able to incorporate such models within formal spatial prioritizations, given the enormous computational size of the problem.

The dual threats of habitat loss and climate change may require solutions that maximize future evolutionary potential and minimize risk from stochastic events (Hoffmann and Sgrò 2011; Hole *et al.* 2011). Such solutions would focus on the conservation of multiple subpopulations and dynamic migratory corridors. Conservation planning software such as MarProb allow information on the probability of species presence or threats to be incorporated into the prioritization algorithm (Carvalho *et al.* 2011) and may prove fruitful.

Critically, existing prioritization approaches allow us to incorporate the costs of conservation actions with ecological information such as connectivity, habitat suitability, or population density (Moilanen *et al.* 2009). A study in California used the conservation planning software Marxan to prioritize a multi-species conservation network for migratory shorebirds and waterfowl (Stralberg *et al.* 2011), taking into account cost information.. Population densities at each site were estimated through a combination of survey data and expert judgment on habitat use, and were used in conjunction with cost information to prioritize sites for conservation action across the region. Conservation targets were set separately for each site (and season) to accommodate potentially distinct populations. While this study considered only the parts of the migrants' life cycle spent within California, this

approach could in principle be extended to design conservation networks across the full life cycle.

Conserving mobile species with incomplete and uncertain information

Given financial and time constraints, an intensive research-driven approach to conservation will not be feasible for the vast majority of migrants, especially where little is known about migratory connectivity. Where information is limited, there are basically three choices for conservationists: investing in activities that improve current knowledge (ie "learning more"), using existing information to estimate the optimal conservation plan, or undertaking a combination of learning while taking action (ie adaptive management; Keith *et al.* 2011). Often, learning more is not the most effective way to achieve conservation outcomes, because of the delay in action, the risk of catastrophic population declines while new knowledge is acquired (Martin *et al.* 2012b), and the fact that resources might be diverted from on-the-ground management (McDonald-Madden *et al.* 2010). The use of decision-theoretic approaches from applied mathematics and artificial intelligence can aid decision making where data are scarce (Martin *et al.* in press). These techniques can also demonstrate how to optimally allocate time and resources between learning and taking action across space and time (Chadès *et al.* 2011). The application of decision science to solve migratory species conservation problems follows the same basic principles as any well-designed prioritization process: (1) define a clear objective (eg what to minimize or maximize); (2) specify a set of conservation actions from which a subset will be chosen as priorities; (3) build a model of how specific conservation actions will help meet the objective; (4) consider resource constraints (ie time and money); and (5) implement decisions in a way that promotes learning (Gregory *et al.* 2012; Game *et al.* 2013).

In practice, information on system behavior (such as migratory connectivity or survival across different parts of the migratory life cycle) is often lacking. In these cases, consultation with experts is proving useful (Martin *et al.* 2012a) and has been used to estimate population size of (Martin *et al.* 2007), habitat use by (Stralberg *et al.* 2011), and connectivity in (Iwamura *et al.* in press) migratory species. Uncertainty in parameter estimates can be accounted for through the use of structured expert elicitation techniques. For instance, imagine that estimates of survival for the monarch butterfly (*Danaus plexippus*) during a portion of its migratory flyway are required to parameterize a population model. To account for uncertainty, we could apply an elicitation process by asking experts to first estimate a range of survival values and then evaluate the probability that survival will fall within that estimate (Speirs-Bridge *et al.* 2010).

Many of the more advanced techniques in decision science have yet to be applied formally to conservation problems associated with mobile species, suggesting possibilities for future applications. For example, it should be possible to design conservation plans that are robust to different plausible patterns of connectivity, or to cases where connectivity changes as a result of threats. Techniques based on decision theory can also highlight what new information would be most critical for improving conservation decision making in a particular situation, so that research effort can be focused on gaining new knowledge most likely to lead to a change in management (Grantham *et al.* 2009; Runge *et al.* 2011; Nicol and Chadès 2012).

Defining an appropriate suite of actions

Conservation planning is about choosing actions, not just choosing sites (Wilson *et al.* 2009; Game *et al.* 2013). For mobile species where movement patterns are unpredictable or changing in space and time, the suite of potential actions may be diverse and complex (Bull *et al.* 2013). In addition to fixed actions in fixed locations, resource managers may need to

implement conservation actions that are ephemeral and depend on the state of the system. State-dependent actions have already been applied to conservation of static species (McCarthy *et al.* 2001; Johnson *et al.* 2011), and are particularly relevant to mobile species. Examples of state- or time-dependent actions might be to limit fisheries near sea turtle rookeries during the breeding season (James *et al.* 2005) or to halt wind-turbine activities during peak bird, bat, or insect migration periods (Drewitt and Langston 2006).

Dynamic alternatives to static protected areas, such as temporary stewardships or seasonally transient protected areas, may need to be considered (Bengtsson *et al.* 2003). These approaches are already used in marine conservation (Somers and Wang 1997; Horwood *et al.* 1998; Cinner *et al.* 2006). For instance, temporary closure of specific areas of South African long-line fisheries has been identified as an effective model for reducing bycatch of nomadic pelagic seabirds with least cost to the long-line fishing industry (Grantham *et al.* 2008). A key challenge for conservation biologists is to identify ways to implement dynamic protection on land where opportunities for dynamic landscape management are limited.

Because of the extensive use of space by many mobile species, whole-landscape management will often be preferable to restricting conservation to the small zones within protected areas. An illustration of a successful whole-landscape management strategy is the conservation of pink-footed geese (*Anser brachyrhynchus*) in Europe (Klaassen *et al.* 2008). Pink-footed geese breed in Norway and winter in Denmark, the Netherlands, and Belgium, with stopover sites in Norway and Denmark. These stopover sites comprise agricultural land, causing conflict between landowners whose crops are damaged and conservation groups wanting to maintain the migration. Conservation of these birds may involve protecting key sites, compensation to farmers within a designated flyway where goose-related damage to crops is accepted, and bird-scaring techniques to limit use of non-target lands by birds. This kind of conservation initiative relies on cooperation among multiple stakeholders and is best suited to managed landscapes, where actions can be arranged dynamically across space and time. In more intact landscapes, or where resources are scarce and threats are more pervasive, more universal actions will likely be required.

Conclusions

Mobile species represent a major challenge for conservation planners. Traditional conservation planning approaches are inadequate for most situations in which species move from place to place, and we urge the development of research that (1) accounts for the dependencies among sites created by migratory connectivity, (2) determines explicitly when more knowledge about migratory connectivity will be useful for conservation, and (3) identifies actions that are dynamic in space and time. Observed rapid declines in mobile species around the world (Kirby *et al.* 2008) suggest that time is running out to achieve the large-scale conservation action necessary to mitigate the loss of these great wildlife spectacles.

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Figures

Figure 1

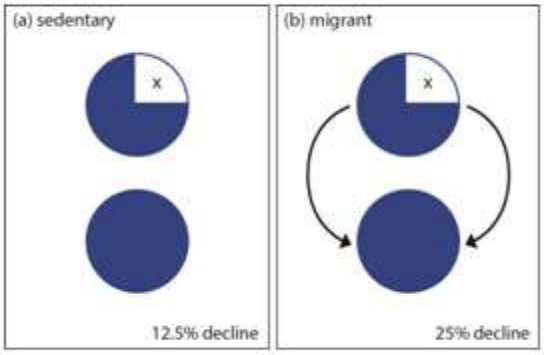

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Figure 1. In this theoretical example, habitat loss has affected one-eighth of the total habitat available to a species that occurs in two patches. If habitat quality and population abundance are evenly distributed within and among patches, we might predict that a sedentary species (a) will decline in total population size by one-eighth as a result of the habitat loss. Where the two patches are linked by migration (b), we might predict a population decline of one-quarter because the entire population passes through the affected patch at some point during its life cycle. If one habitat patch is lost altogether, extinction of the migratory species will result.

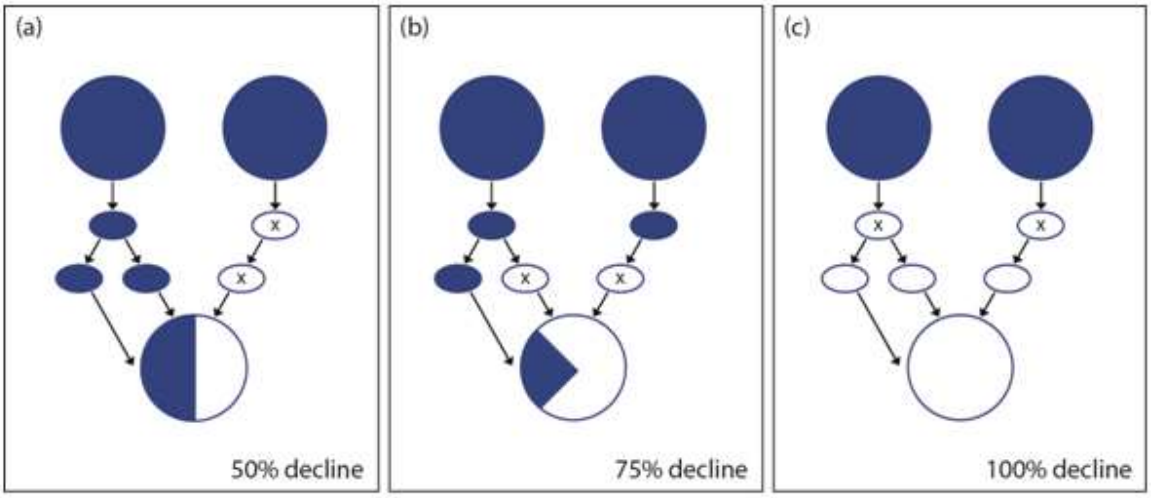

Figure 2. The use of migration corridors or stopover sites makes mobile species vulnerable to changes in habitat quality in relatively small and briefly used areas. A decline in quality or loss of access to small sites can result in disproportionately large population losses. Panels (a), (b), and (c) represent scenarios in which two breeding populations of a migratory species pass through stopover sites en route to overlapping non-breeding sites. In each of the three scenarios, only two stopover sites are lost; however, the population implications are highly dependent on the spatial configuration of that loss. Understanding migratory connectivity can be crucial to managing mobile species effectively.

Figure 3. Eastern curlews (*Numenius madagascariensis*) migrate each year from the Arctic to Australia, stopping to feed and rest at tidal flats across the East Asian–Australasian Flyway (EAAF). The species has recently been uplisted to globally Vulnerable, and habitats across its migration and non-breeding range are susceptible to degradation and loss through prey species declines, reclamation, changes in sedimentation patterns, and sea-level rise. Managing these multiple interacting threats requires conservation actions that take account of migratory connectivity, and that operate in many countries across the Flyway. One important conservation initiative has been the formation of the EAAF Partnership, an alliance of 30 governments and non-governmental organizations working across the region. The Partnership has already listed a network of more than 100 important sites across the Flyway in 16 countries.

Image credit:

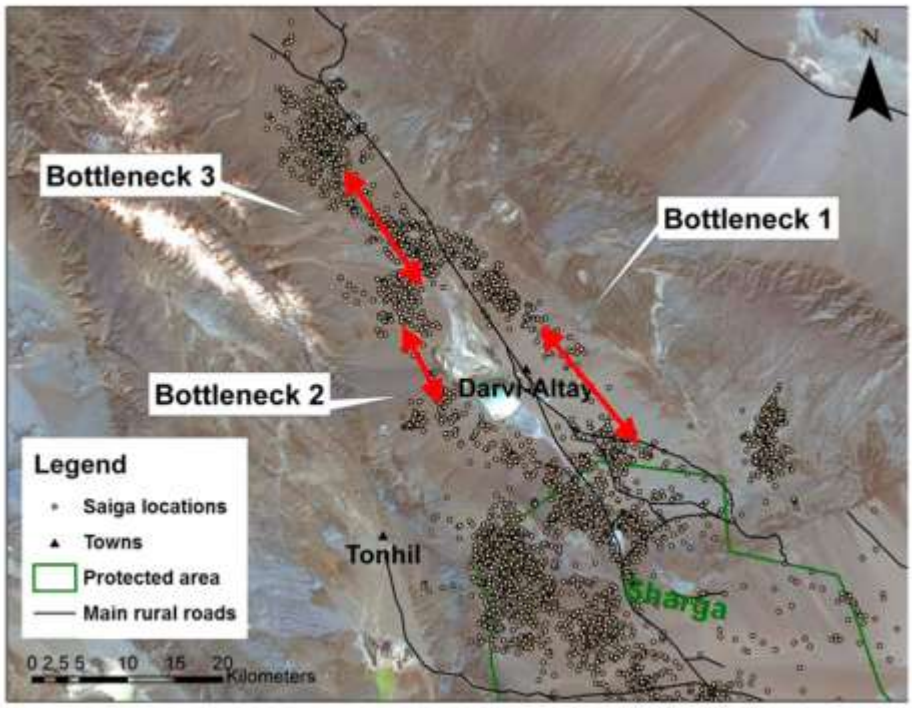

Figure 4. Analysis of tracking data for Mongolian saiga (*Saiga tatarica mongolica*) reveals the presence of bottlenecks in their migration. Migration is funneled by geographical constraints through a small valley, leaving this migration pathway at risk of being blocked off by changing human use. As anti-poaching measures improve prospects for this species, maintaining these migration pathways will be essential for the long-term management of these animals. Adapted from Berger *et al.* (2008).

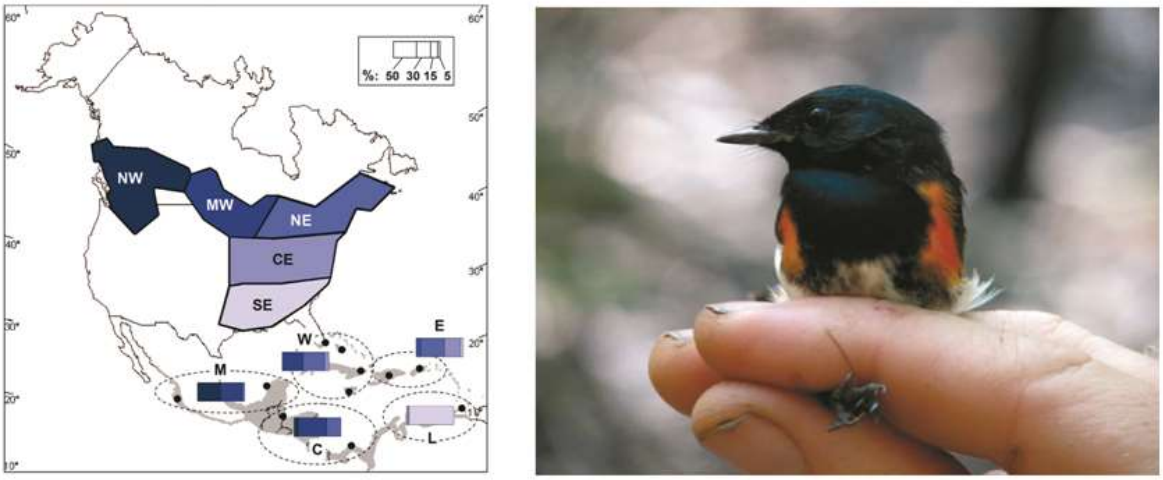

Figure 5. Stable isotope analysis was used to map the spatial connections between five non-breeding populations and five breeding regions for the American redstart (*Setophaga ruticilla*). This map shows the distribution of the most likely breeding region (NW = Northwest; MW = Midwest; NE = Northeast; CE = Central-East; SE = Southeast) for individual redstarts at each non-breeding region (M = Mexico; C = Central America; W = Western Greater Antilles; E = Eastern Greater Antilles; L = Lesser Antilles). Black dots indicate sampling locations and bars indicate the proportion of individuals assigned to each

breeding region. For example, the entire Northwest breeding population migrates to Mexico; failing to protect non-breeding habitat in Mexico will therefore likely doom the Northwest breeding population of redstarts to extinction. Adapted from Martin *et al.* (2007).

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Table 1. Descriptions of large-scale animal movements

Migration	A cyclic and predictable movement beyond a home range. From altitudinal migration up and down a mountainside or stream, to partial migration where certain populations migrate and others remain sedentary, and differential migration where certain groups within a population such as females, males, or juveniles migrate. May entail a single direct trip or a gradual journey using stopover locations. Breeding and non-breeding grounds can be spatially distinct or overlapping.
Nomadism	Wandering movements without fixed breeding grounds, though often some seasonal directionality (Dean 2004). Breeding occurs when and where conditions permit, rather than in fixed times and places. Nomadic species may become sedentary at certain times in their life cycle, or under particular climatic conditions, reverting to nomadic movements as resource distributions change. Often associated with arid regions, nomads commonly occur where there is high inter-annual variability in resource availability, such as pelagic species reliant on moving fish stocks and tropical forest animals that depend on flowering or fruiting events.
Irruption	In some species, normally sedentary individuals occasionally undertake long-distance movements, often in response to unusual spikes or troughs in resource availability. Examples include boreal forest birds such as pine grosbeaks (*Pinicola enucleator*) and spotted nutcracker (*Nucifraga caryocatactes*). These expansions may occur as a shift in breeding distribution to take advantage of a resource boom (irruption coincides with boom), to avoid a resource failure such as food shortage, or as a competition-driven dispersal event of unusually high numbers of juveniles (irruption post-boom).
Intergenerational relays	Several insects, such as the monarch butterfly (*Danaus plexippus*) and North American green darner dragonfly (*Anax junius*), undergo regular migrations over multiple generations. Monarchs undergo a multi-generational migration from their non-breeding grounds in Mexico to their most northern breeding sites in Canada, breeding up to four times during the annual cycle (Flockhart *et al.* 2013). In the case of the green darner, once the adults complete the southward migration, they die and the next generation begins the northward movement during the following spring (Russell *et al.* 1998).